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THE MECHANISMS OF CARAPACIAL AND PLASTRAL HINGES IN CHELONIANS

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Deraniyagala (1939) described the carapace and plastron of *Lissemys* and reported that there are two movable corselets in the carapace and four in the plastron. In the carapace the prenuchal is loosely connected to the anterior border of the nuchal by a thick ligament. This anterior corselet is moved downwards and acts as a valve. The last two marginals form a posterior movable valve in the carapace. In the plastron, the epiplastral lobe acts as an anterior plastral valve, and a small portion of the posterior part of the plastron demarcated by a transverse groove forms the posterior plastral valve. Besides these, there is a pair of cutaneous flaps which are used as valves to cover the posterior limbs after they are retracted under the shell. These flaps are known as the femoral valves. Presence of the cutaneous femoral valves is a distinguishing character of the subfamily Cyclanorbinae, in which the three genera *Lissemys*, *Cyclanorbis* and *Cycloderma* are grouped. Hasan (1941) worked out the shell-closing mechanism and described the principal muscles responsible for the movements of the six movable parts in *Lissemys*. George and Shah (1955), while working on the musculature of *Lissemys*, gave possible homologies of the muscles described by Hasan.

In the present study an attempt is made to describe the closing mechanism of the shell in most[1] of the chelonians in which part of the plastron or carapace is movable and acts as a valve. Careful dissections of the muscles involved in the movements of the plastral lobes or the carapace parts were made of the following chelonians: *Cuora amboinensis, Emys orbicularis, Emydoidea blandingi, Terrapene mexicana yucatana, T. carolina carolina, T. c. baurii, T. c. triunguis, T. ornata, Testudo graeca, T. hermanni, T. kleinmanni, Kinixys erosa, Kinosternon baurii, K. cruentatum, K. flavescens spooneri, K. herrerai, K. leucostomum, K. scorpioides scorpioides, K. subrubrum, Sternotherus carinatus minor, S. odoratus, Cycloderma frenatum, Pelusios adansoni, P. carinatus, P. castaneus, P. nanus, P. subniger.* All specimens examined are in the collection of the Museum of Comparative Zoology.

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[1] No adult was available of *Notochelys platynota* in which an indistinct transverse hinge has been reported. Similarly there is only a juvenile at hand of *Pyxis arachnoides*. Siebenrock has described in this species a mobile anterior plastral lobe in which the entoplastron becomes involved. Since hinges only develop with age, it has not been possible to investigate hinge mechanisms in these species.

Only two genera of the chelonians listed above, viz., *Cycloderma* and *Kinixys,* show some part of their carapace movable; the others have some part or parts of their plastra movable. In this regard all the chelonians used for the present study could be classified in four different groups:

The first group has only the anterior plastral lobe hinged and capable of valvular movements. The hinge is usually situated at the joint of hyo- and hypoplastral plates. The species of emydines examined show this condition.

The second group includes those that have only their posterior plastral lobes movable. The posterior plastral lobe is hinged at the level of the joint of the hypo- and xiphiplastral plates. This group is composed of the species of *Testudo* cited above.

The third group includes those which have both anterior and posterior plastral lobes movable. The kinosternines examined belong here.

The fourth group consists of the members of the subfamily Cyclanorbinae in which besides the movable anterior and posterior plastral lobes there are the two cutaneous femoral valves.

MOVEMENTS OF CARAPACE VALVES

In *Cycloderma* and *Cyclanorbis,* as in *Lissemys,* the prenuchal is movable. Hasan (1941) has described as the *M. nuchoprenuchalis* the muscle which is responsible for the movements of the prenuchal. This muscle arises from the under surface of the nuchal and is inserted on the posterior half of the under surface of the prenuchal. When this muscle contracts, the prenuchal is pulled downwards and acts as a small valve to close the shell after the head and the fore limbs are drawn under the shell and the anterior lobe of the plastron is lifted upwards. George and Shah

(1955) homologised this muscle with that part of the *spinalis-semispinalis* system occurring in this region. In no other chelonians are there such movable prenuchals.

The last two marginals in *Cycloderma* and *Cyclanorbis,* like those in *Lissemys,* are movable and act as a supracaudal valve. The *margino-infracaudales* are responsible for the downward pull (Hasan 1941). These muscles arise from the undersurface of the marginals and are inserted on the flexible subcaudal valve of the plastron. When these muscles contract the two movable marginals are pulled downwards and at the same time the subcaudal valve of the plastron is pulled upwards. The joint action of these two valves, i.e. the subcaudal and supracaudal valves, close the shell from behind and protect the tail and surrounding soft parts. These muscles are homologised with part of the *flexor caudae superficialis* by George and Shah (1955).

In *Kinixys erosa* an entirely different situation is present. Siebenrock (1916) has described the morphological features of the hinged carapace of this species in great detail. Briefly, however, it may be mentioned that the hinge is at the level of the fourth and fifth costal plates, the posterior part of the carapace being moved up and down like a valve at this point. This movement of such a large part of the carapace is unique to this genus.

The closing movement is brought about in the following manner. First the head and the neck are pulled under the shell as a result of the contraction of the *retrahens capitis collique*, the *rectus capitis cervico-plastralis* and *rectus cervicis* muscles. Of these muscles the *retrahens capitis collique* is the principal muscle responsible for the withdrawal of the head and the neck. The main part of this muscle in *Kinixys erosa* arises from the body of the seventh and eighth dorsal vertebrae and the undersurface of the costal plates near these vertebrae. The muscle inserts on the cervical vertebrae and on the base of the skull at its ventral side. After the head and neck are retracted fully, the muscle contracts still further and this additional contraction pulls the hinged posterior part of the carapace downwards and closes the shell from behind. In addition, the pelvic girdle muscles, i.e. the *attrahens pelvium,* also help in pulling the hinged part of the carapace downward. The *attrahens pelvium* is very highly developed in this genus and when it contracts the entire pelvic girdle is pulled forward, and since the girdle is firmly attached to the carapace the carapace is pulled with it. Although this pull is not so great as the one exerted by the *retrahens capitis collique* it does contribute to the movement. A few muscles of the legs, i.e. the *ilio-tibialis* and *ilio-femoralis* which in part arise from the costal plate, also exert a pull on the carapace after the legs are fully retracted under the shell. Thus a combined pull resulting from the contraction of all these muscles is responsible for bringing about the valvular movements of the posterior hinged part of the carapace.

MOVEMENTS OF THE PLASTRAL LOBES

Anterior plastral valve: The anterior plastral lobe is hinged at the level of the hyo-hypoplastral joint in *Emys orbicularis, Emydoidea blandingii, Cuora amboinensis, Terrapene mexicana yucatana, T. carolina carolina, T. c. baurii, T. c. triunguis, T. ornata, Pelusios subniger, P. castaneus, P. carinatus* and *P. adansonii.* This anterior plastral lobe can be moved upwards like a valve which shuts off the shell in front after the head, neck and the fore limbs are retracted. This upward movement of the anterior plastral lobe is brought about in the following manner: After the head, neck and the fore limbs are retracted, the clavicular part of the *deltoideus* muscle contracts and pulls the plastral lobe upwards. The anterior part of the *pectoralis* muscle, which has its origin from the plastral lobe, also on contraction pulls the plastral lobe upward. Some part of the *scalenus* muscle which is inserted on the border of the plastral lobe helps in pulling the lobe upward. The precoracoid cartilage is attached to the entoplastral plate by a thick ligament and so when the whole girdle is rotated forward with the scapula acting as a fixed point the precoracoid and the coracoid which normally lie in a horizontal plane come now into an inclined plane with the precoracoid lifted upwards. Along with these the plastral lobe also gets pulled upwards and thus the rotation of the girdle helps in lifting the plastral lobe. These combined actions bring about the valvular movement of the anterior plastral lobe.

Normally the anterior plastral valve has a straight transverse hinge. This disposition of the hinge is very necessary for free valvular movements of the plastral lobe. But to this normal condition there is an exception in *Pelusios adansonii.* In this animal the hinge is not a straight transverse one but is V-shaped with the apex directed posteriorly. Because of this type of hinge the valvular movements of the anterior plastral lobe in this animal are very restricted compared to those possible with a straight transversely placed hinged.

Posterior plastral valve: A hinged posterior plastral lobe occurs in *Testudo kleinmanni*, *Testudo graeca* and *Testudo hermanni*. The hinge is at the level of the hypo-xiphiplastral joint and is also transversely placed. The posterior plastral lobe is pulled upward as a result of the contraction of the *retrahens pelvium* muscle of the pelvic girdle. This muscle arises from the spine of the pubis and is inserted on the entire inner surface of the xiphiplastral plate. In these animals the muscle is more highly developed than in forms which do not have a hinged posterior plastral lobe. Besides the action of the *retrahens pelvium* muscle the skin connecting the legs and the plastron exerts some pull on the plastral lobe which helps in pulling it upward.

Anterior and posterior plastral lobes: *Kinosternon subrubrum*, *K. flavescens spooneri*, *K. leucostomum*, *K. scorpioides scorpioides*, *K. baurii*, *K. cruentatum*, *K. herrerai*, *Sternotherus carinatus minor*, and *Sternotherus odoratus* possess anterior as well as posterior plastral lobes which are hinged and are capable of valvular movements. The upward movements of these two plastral lobes are brought about in the same way as described separately in the first two groups which had only one lobe, whether anterior or posterior, movable.

In *Kinosternon*, as far as the anterior plastral lobe is concerned, there is an additional factor pulling the plastral lobe upward. There are thick tendons which loosely connect the fourth, fifth and sixth cervical vertebrae with the plastral lobe. The point of attachment of these tendons on the plastral lobe is at the border of the epiplastral plates. When the head and the neck are pulled under the shell as a result of the contraction of the *retrahens capitis collique* (the main retractor of the head and the neck), an indirect pull is exerted on the plastral lobe because the latter is connected by thick tendons with the cervical vertebrae. Such a type of tendinous connection between the cervical vertebrae and the plastron is not met with in any of the other chelonians studied.

The *Terrapene* species examined have been placed in the first group in which only one anterior plastral lobe is hinged and movable like a valve. These species, however. require special attention since, although there is no true posterior plastral hinge, the posterior lobe is capable of being pulled dorsally and can close the shell posteriorly as efficiently as in those which have the posterior plastral lobe hinge. Here the bridge between the carapace and the plastron is very short and a large portion of the posterior part of the plastron is left unsupported. The *retrahens* *pelvium* muscle in this animal is very highly developed and so when it contracts the posterior plastral border is lifted upward. This lifting occurs because the plastral plate bends under the pull exerted by the *retrahens pelvium* muscle. In this way, although there is no hinge at the level of the hypo- and xiphiplastral joint, the plastral plate closes the shell from behind, after the hind limbs and the tail are retracted within the shell.

Four plastral valves: The fourth group of the chelonians includes those which possess four plastral valves capable of valvular movements — the members of the subfamily Cyclanorbinae — *Lissemys, Cyclanorbis* and *Cycloderma*. Here the anterior plastral lobe is not as well demarcated and hinged as in the animals described above, but since the plastron is soft the movement is effected at the level of the posterior border of the entoplastral plate and the anterior border of the fused hyo-hypoplastral plate. This anterior plastral valve is moved upward by the contraction of the specially developed muscle — the *nucho-plastralis* (Hasan, 1941), described as the *trapezius* by George and Shah (1955). This muscle arises from the nuchal plate, runs along the base of the neck, and is inserted on the epiplastral plate. When the *trapezius* (=*nucho-plastralis*) muscles contract the anterior plastral lobe is lifted upward to close the shell. In addition, other muscles are also taking part in the closing mechanism of the anterior plastral lobe; these are: the clavicular part of the *deltoideus,* the *rectus capitis cervico-plastralis,* and the part of the *pectoralis* muscle which has its origin on the movable part of the plastron. The skin connecting the legs and the plastron also exerts some pull after the legs are retracted under the shell. The *trapezius* muscle is found only in the Trionychidae. Thus, though the anterior plastral lobe cannot be completely closed in *Trionyx gangeticus,* to a certain extent it can be lifted up to protect the retracted head, neck and fore limb. In this animal, as in the Cyclanorbinae, the *trapezius* muscle is present and works in a fashion similar to that in *Lissemys* (George and Shah 1955).

The infracaudal valve in all the members of the subfamily Cyclanorbinae is a small posterior part of the plastron which is demarcated by a transverse groove and which lies behind the xiphiplastral plates. Here also there is no regular hinged condition. Part of the *flexor caudae superficialis* muscle described for the closing mechanism of the supracaudal valve in the carapace of these animals is used for moving the infracaudal valve upward. Thus, when this muscle contracts the supracaudal as well as the infracaudal valves are moved in opposite directions towards each other to close the shell posteriorly.

For the protection of the hind limbs in these animals an extra pair of cutaneous flaps is developed. These are known as the femoral valves. Each femoral valve is more or less hinged with the side of the xiphiplastral plates and is capable of valvular movements. The closure of the femoral valves is brought about when the ligament connecting the shank of the leg and the valve is tensed, as the legs are retracted under the shell. The skin connecting the legs and the valves also exerts some pull on the valves when the skin is drawn in as the legs are pulled under the shell.

Finally, it may be said that some chelonians have developed certain features like movable plastral or carapace parts by which they can close themselves in a box to protect their soft parts. Besides this, wherever the posterior plastral lobe or the posterior part of the carapace is movable, this capacity for movement also serves to facilitate the egg-laying process by widening the gap between the carapace and the plastron.

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ABBREVIATIONS

At.P.	Attrahens pelvium
At.P.′	Area of origin of attrahens pelvium
Car.	Carapace
C.Carp.	The position of the posterior hinged part of carapace in *Kinixys* when shell is completely closed
C.Dl.	Clavicular part of deltoideus
C.Dl.′	Area of origin of clavicular deltoideus
C.S.Isc.	Cut surface of ischium
C.S.Isc.′	Area of cut surface of ischium where it is fused with plastron
C.S.P.Isc.	Cut surface of pubo-ischial joint which is fused with plastron
C.S.P.Isc.′	Area of pubo-ischial attachment on plastron
F.C.S.	Part of flexor caudae superficialis
F.C.S.′	Area of insertion of F.C.S. on plastron
F.V.	Femoral valve
H.A.P.	Hinged joint of the posterior plastral lobe
H.A.P.′	Place of valvular movement of the anterior plastral lobe in *Lissemys*
H.P.P.	Hinged joint of the posterior plastral lobe
H.P.P.′	Place of valvular movement of the subcaudal valve of plastron in *Lissemys*
J.Car.	Hinged joint in carapace in *Kinixys*
P.	Pectoralis
P.′	Area of origin of pectoralis
P.C.Ca.	Precoracoid cartilage
P.G.	Pelvic girdle
P.G.′	Shifted position of pelvic girdle in *Kinixys* when the shell is completely closed

Pl.	Plastron
R.Carp.	The position of the posterior hinged part of the carapace in *Kinixys* when the shell is fully opened
R.C.C.	Retrahens capitis collique
R.C.C.P.	Rectus capitis cervico-plastralis
R.C.C.P.′	Area of origin of rectus capitis cervico-plastralis
Rt.P.	Retrahens pelvium
Rt.P.′	Area of origin of retrahens pelvium
S.Dl.	Scapular part of deltoideus
Sk.C.	Skin connection between the two hinged parts of the carapace of *Kinixys*
Tn.	Tendons connecting cervical vertebrae with plastron
Tn.′	Place of insertion of the tendons on the plastron
Tr.	Trapezius
Tr.′	Area of insertion of trapezius

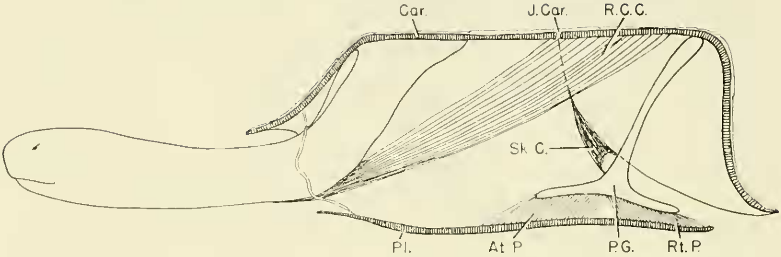

Fig. 1. *Kinixys erosa:* Side view showing extended neck and the position of the muscles, the hinged posterior part of carapace and the pelvic girdle when the shell is open.

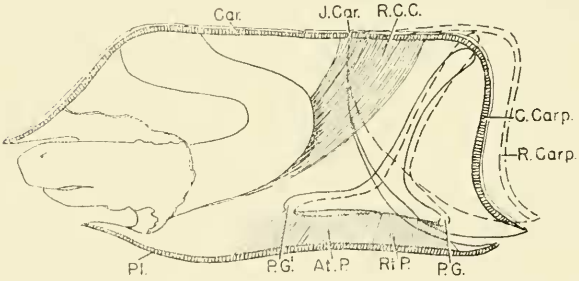

Fig. 2. *Kinixys erosa:* Side view showing the retracted head and neck, the contracted muscles and the shifted position of the pelvic girdle when the shell is closed.

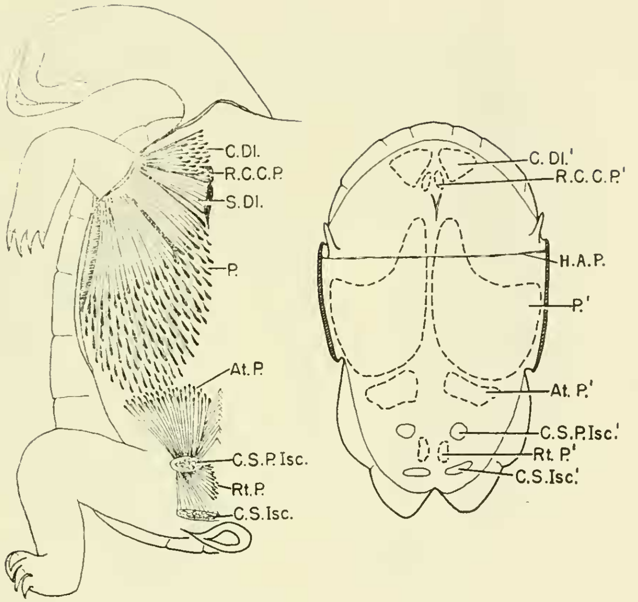

Fig. 3. *Pelusios subniger: Left,* the superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.

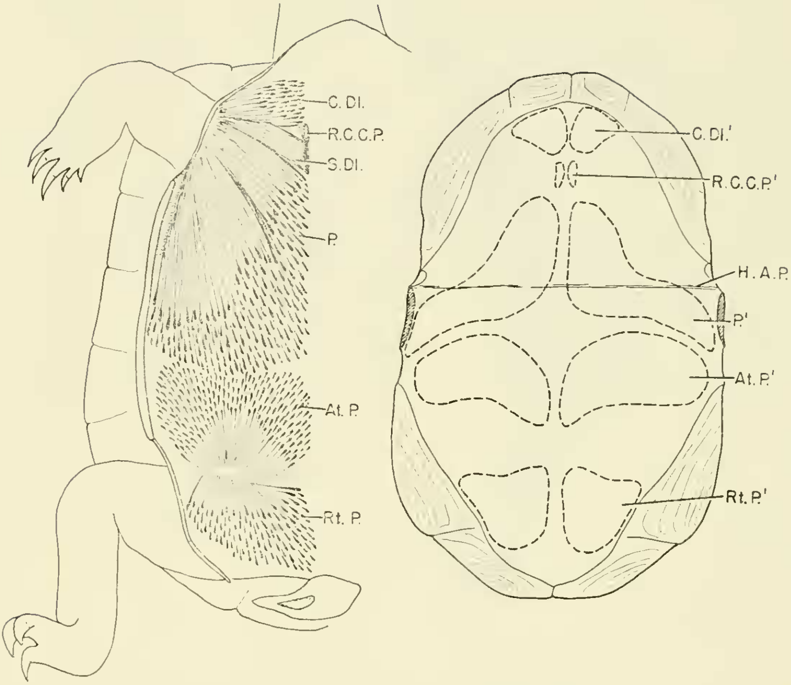

Fig. 4. *Terrapene carolina carolina: Left,* the superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.

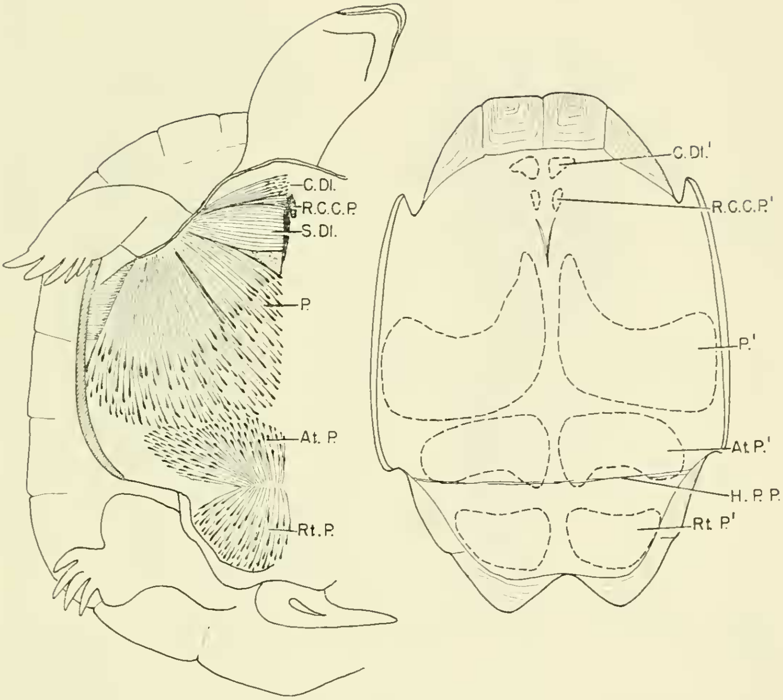

Fig. 5. *Testudo hermanni: Left,* the superficial muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of the various muscles.

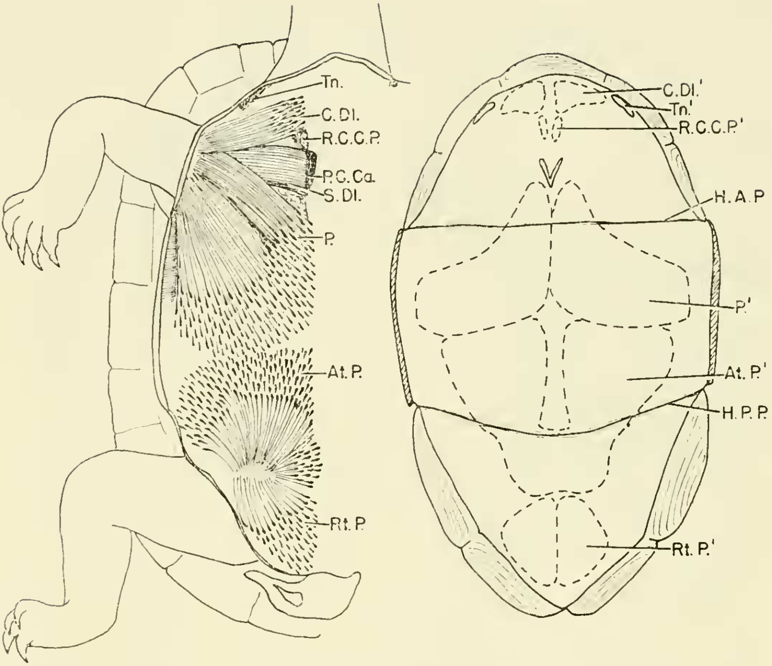

Fig. 6. *Sternotherus carinatus minor: Left,* the superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.

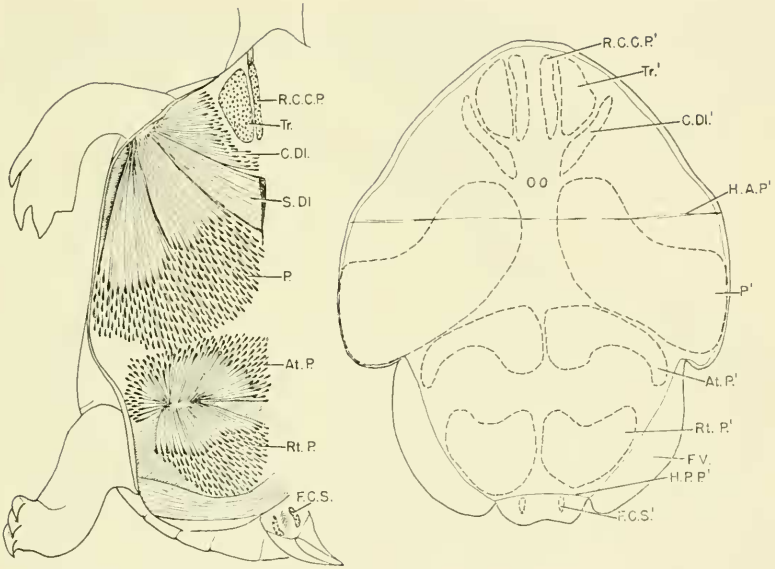

Fig. 7. *Lissemys punctata: Left,* superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.